

On the enigmatic *Sinonemestrius* Hong & Wang, 1990, with description of a new species based on a complete fossil fly (Diptera, Brachycera, Tabanomorpha, Heterostomidae)

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Abstract

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A new species of *Sinonemestrius* Hong & Wang, 1990 is described and illustrated based on a complete compression fossil of the fly. Currently placed in Rhagionemestriidae or Xylophagidae, the present study concludes that the morphology of the new find indicates that *Sinonemestrius* is a heterostomid genus within Tabanomorpha. The placement of *Ahirmoneura neimengguensis* K-y Zhang et al., 2008 is reassessed. It demonstrates close similarities in body structure and wing venation to those of *Sinonemestrius*, and can be provisionally transferred from Nemestrinidae to Heterostomidae: Sinonemestriinae.

Introduction

The Jehol biota (*sensu lato*) constitutes a suite of fossil plants and animals that lived during the Early Cretaceous in eastern- and north-eastern Asia (J-f Zhang 1992). As in the Lower Cretaceous Yixian Formation in Beipiao City of Liaoning Province, China (Ren and Guo 1995, Ren 1998), the order Diptera (true flies) is also well represented in the Lower Cretaceous of the Laiyang Formation in Laiyang City, Shandong Province, China. The suborder Brachycera is abundant. In the author's collection – about one half of the Diptera found is composed of Eremochaetidae (eremochaetid flies), Xylophagidae (awl-flies), Stratiomyidae (soldier flies), Nemestrinidae (tangle-veined flies), Tabanidae (horseflies), Athericidae (water snipe-flies), Rhagionidae (snipe flies), Empidi-

dae (dance flies), Protapioceridae (protapiocerid flies), Platypezidae (flat-footed flies) and Ironomyiidae (ironic flies), etc. Among them, only a few taxa have been described (J-f Zhang 1987, 2012, 2014, 2015, Hong and Wang 1988, 1990, J-f Zhang et al. 1993).

A rare and unusual nemestrinid-like brachyceran wing from the Laiyang Formation in the vicinity of Tuanwang Village, Laiyang, Shandong, China was described by Hong and Wang (1990) and named *Sinonemestrius tuanwangensis* Hong & Wang, 1990. The taxonomy and systematics of this enigmatic form have been much debated. It has a history of controversial taxonomy that has placed this nemestrinid taxon in up to four separate families (Hong and Wang 1990, Nagatomi and Yang 1998, Jarzembowski and Mostovski 2000, Mostovski and Martínez-Delclòs 2000, Nel 2010, Grimaldi 2016). This problem

is resolved here based on a new, complete compression of a sinonemestriid fly originating from the same fossil locality (Laiyang Formation in the vicinity of Tuanwang Village). In addition, the placement of another nemestrinid-like brachyceran, *Ahirmoneura neimengguensis* K-y Zhang et al., 2008, is reassessed. It could be related to Heterostomidae:Sinonemestriinae as it demonstrates close similarities in body structure and wing venation to those of *Sinonemestrius* Hong & Wang, 1990 rather than tangle-veined flies (see Remarks in Taxonomy below).

Material and methods

Material. The holotype of a shale fossil compression of a male sinonemestriid fly described herein is deposited in the collections of the Nanjing Institute of Geology and Palaeontology (NIGP), the Chinese Academy of Sciences, no. NIGP L91803. The fly-bearing sedimentary rocks of the Laiyang Formation are located near the village of Tuanwang, Laiyang City, Shandong Province, China.

Illustrations. Specimen descriptions, photomicrographs and line drawings were done with the application of glycerol to the surface of the specimens. The line drawings were produced with the aid of a camera lucida and the digital photomicrographs were taken using a stereomicroscope (Leica M205C).

Wing venation terminology here follows Wootton and Ennos (1989) and Shcherbakov et al. (1995). The cell traditionally named the anal cell is here considered to be the cubital cell. The following standard abbreviations are used: Sc, subcosta; R1, first radius; R2+3, second and third radius; R4, fourth radius; R4+5, fourth and fifth radius; bR4+5, basal section of R4+5; dR4+5, distal section of R4+5; R5, fifth radius; Rs, radial sector; M1, first media; M2, second media; M3, third media; M4, fourth media; CuA, cubitus anterior; CuP, cubitus posterior; r-m, crossvein between radius and media; m-m, crossvein between media; m-cu, crossvein between media and cubitus; bm, basal cell of media; br, basal cell of radius; cu, cubital cell; dc, discal cell.

Colour described here refers to that of the fossil, where patterning is preserved, not the hue of the live fly.

Taxonomy

Heterostomidae Nagatomi, 1977

Sinonemestriinae Nagatomi & Yang, 1998, stat. nov.

***Sinonemestrius* Hong & Wang, 1990**

Type-species. *Sinonemestrius tuanwangensis* Hong & Wang, 1990

Included species. *Sinonemestrius akirai* Jarzembowski & Mostovski, 2000 and *Sinonemestrius completus* sp. n., besides the type species *Sinonemestrius tuanwangensis* Hong & Wang, 1990.

Diagnosis. Medium-sized flies with robust build; body covered with dense hairs but devoid of setae; head moderately large, semiglobose, shorter and narrower than thorax, comprised mostly of the eyes; eyes holoptic in male, hind margin with emargination; antenna short, corneous, with eight-segmented flagellum, first flagellomere swollen, stylus (or arista) absent; wing membrane with markings; R1 relatively short; R2+3 curved, relatively short, ending at, or near to, R1 tip; R4 usually sigmoidal; R5 nearly straight, aligned with stem of R4+5; crossvein r-m present; R5 or M1 ending at wing tip; M2 ending behind wing tip; cell cu (traditionally anal cell) open; metatibia with two very short spurs; empodium present.

Remarks. The original generic diagnosis was defined based on wing impressions (Hong and Wang 1990, Jarzembowski and Mostovski 2000). A revised and supplemented diagnosis including some critical structures of the body is proposed here based on a complete compression fossil of the fly.

Based on a single impression fossil of a nemestrinid-like fly from the Jurassic of the Daohugou biota in the vicinity of Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, China, K-y Zhang et al. (2008) erected a new genus *Ahirmoneura* (type species: *Ahirmoneura neimengguensis* K-y Zhang et al., 2008). They classified this genus in Nemestrinidae. It certainly resembles representatives of the extinct nemestrinid subfamily Archinemestriinae and even some living tangle-veined flies in that R4, R5, M1 and M2 end near to the wing tip. Nevertheless, the clearly short R1 and the absence of the so-called diagonal vein exclude this genus from the Nemestrinidae. In many features (including body structures and wing venation), *Ahirmoneura* resembles *Sinonemestrius* (lack of setae on the body; hemispherical head; elongate-ovate abdomen covered with hairs; very short R1; R4, R5, M1 and M2 ending near to wing tip; and the so-called diagonal vein absent). It should be noted that the wing venation of *Ahirmoneura neimengguensis* demonstrates very close similarities to that of *Sinonemestrius akirai* (Figs 3C, D). The former species differs from the latter one only by the longer, straight R2+3, which ends at C far apart from the end of R1, M2 (instead of M1) ends just at the wing tip and r-m meets the anterior margin of the discal cell near to its base. Unfortunately, the crucial structure of the antenna of *Ahirmoneura neimengguensis* is unknown. Until a new find (including antenna) of this species is available, *Ahirmoneura* can only be provisionally assigned to Heterostomidae: Sinonemestriinae.

***Sinonemestrius completus* sp. n.**

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Figs 1–3

Diagnosis. Similar to *Sinonemestrius tuanwangensis*, but R2+3 smoothly curved downwards and parallel to R1, ending at C instead of R1 end; fork of R4+5 distinctly distad

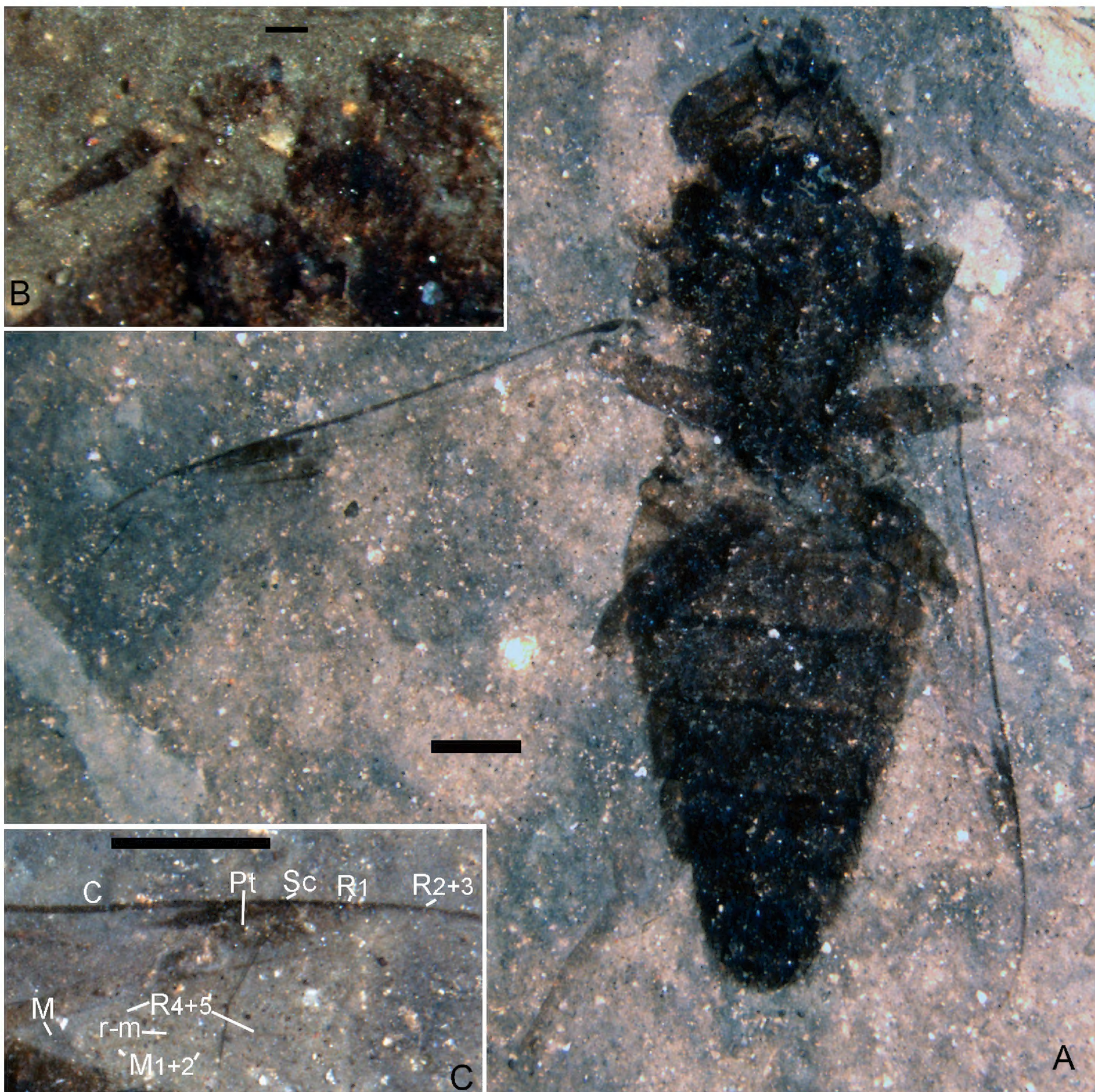


Figure 1. *Sinonemestrius completus* sp. n., no. NIGP L91803, holotype, photographs, male, dorsal view. **A** habitus, **B** antenna, **C** enlarged portions of right wing. Scale bars: 1 mm (**A**, **C**) and 0.1 mm (**B**).

to fork of M1+2; crossvein r-m meeting anterior margin of discal cell basad to its midlength; wing membrane with few markings (only limited to “Pt” and below it).

Description. Male medium-sized flies. Female unknown. Head moderately large, semiglobose, slightly narrower, but distinctly shorter, than thorax; vertex plus frons more or less flattened; eyes large, holoptic, covering almost entire head; antenna shorter than head, scape subquadrate, slightly wider than long, pedicel much shorter, less than one half of scape length, more than twice wider than long, first flagellomere extremely swollen, nearly pyriform, much longer and wider than scape and pedicel combined, less than twice as long as wide, other flagellomeres gradually tapering apically, about three times as long as first flagellomere (Figs 1B, 2B).

Thorax subovate, mesoscutum longer than wide, slightly wider than head; scutellum small, rounded apically, distinctly wider than long; wing nearly three times as long as wide; C thickened but thinned just at wing tip; R1 slightly curved smoothly, about three-fourths of wing length; Rs arising from R more or less late, about at one-third of wing length; R2+3 parallel to R1, ending at C; “Pt” well developed, another brown marking between R1 and R2+3 below base of “Pt” present (Figs 1A, C, 2C); Rs stem shorter than bR4+5, bR4+5 shorter than dR4+5, fork of R4+5 clearly distad to level of fork of M1+2; r-m meeting anterior margin of discal cell basad to its midlength, bM1+2 about one half of dM1+2 length; br cell nearly as long as, but obviously narrower than, bm cell; discal cell nearly pentagonal, relatively short, about

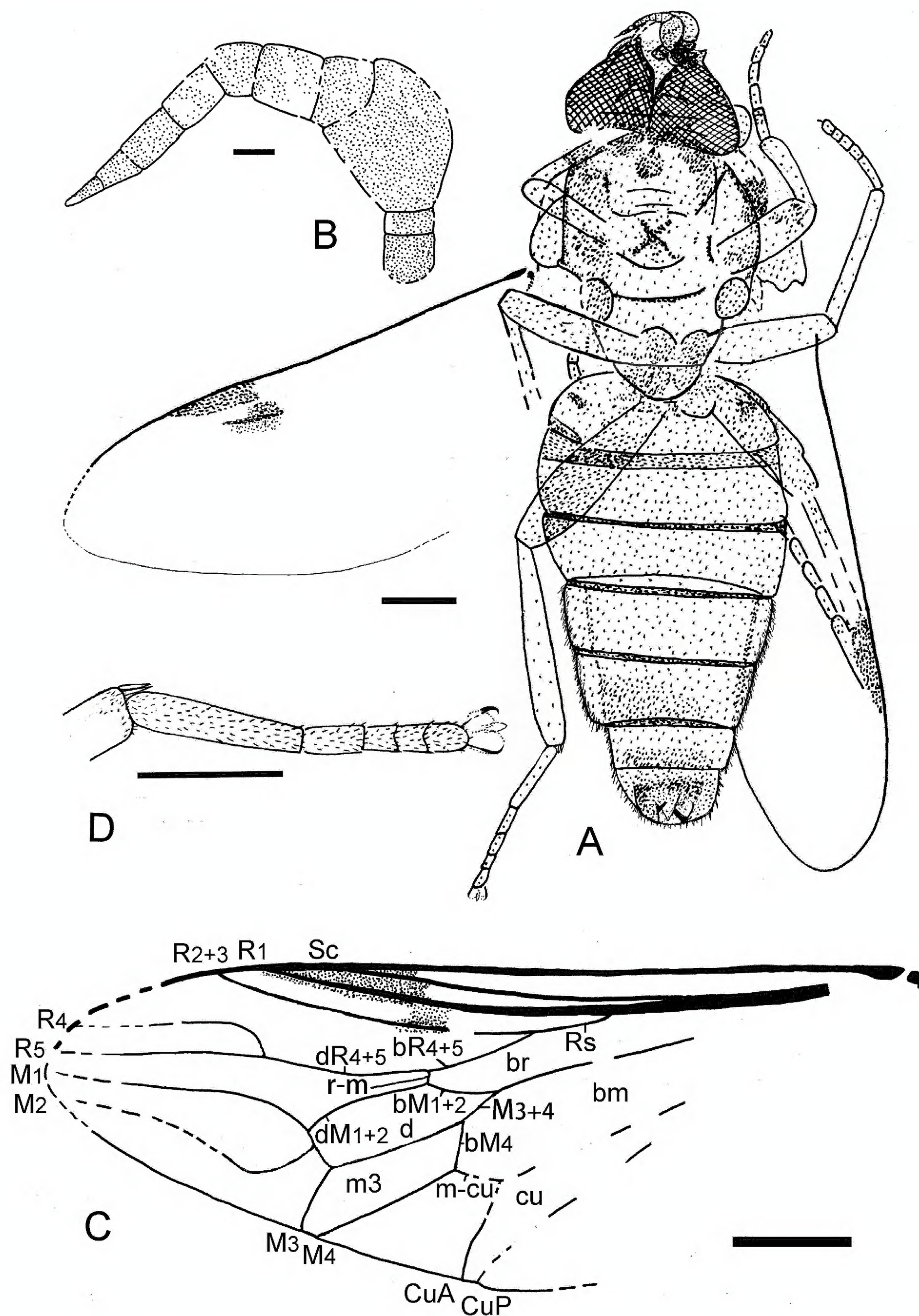


Figure 2. *Sinonemestrius completus* sp. n., no. NIGP L91803, line drawings of holotype. A habitus (wing venation omitted), B antenna, C left wing, D tarsus of left hindleg. Scale bars: 1 mm (A, C, D) and 0.1 mm (B).

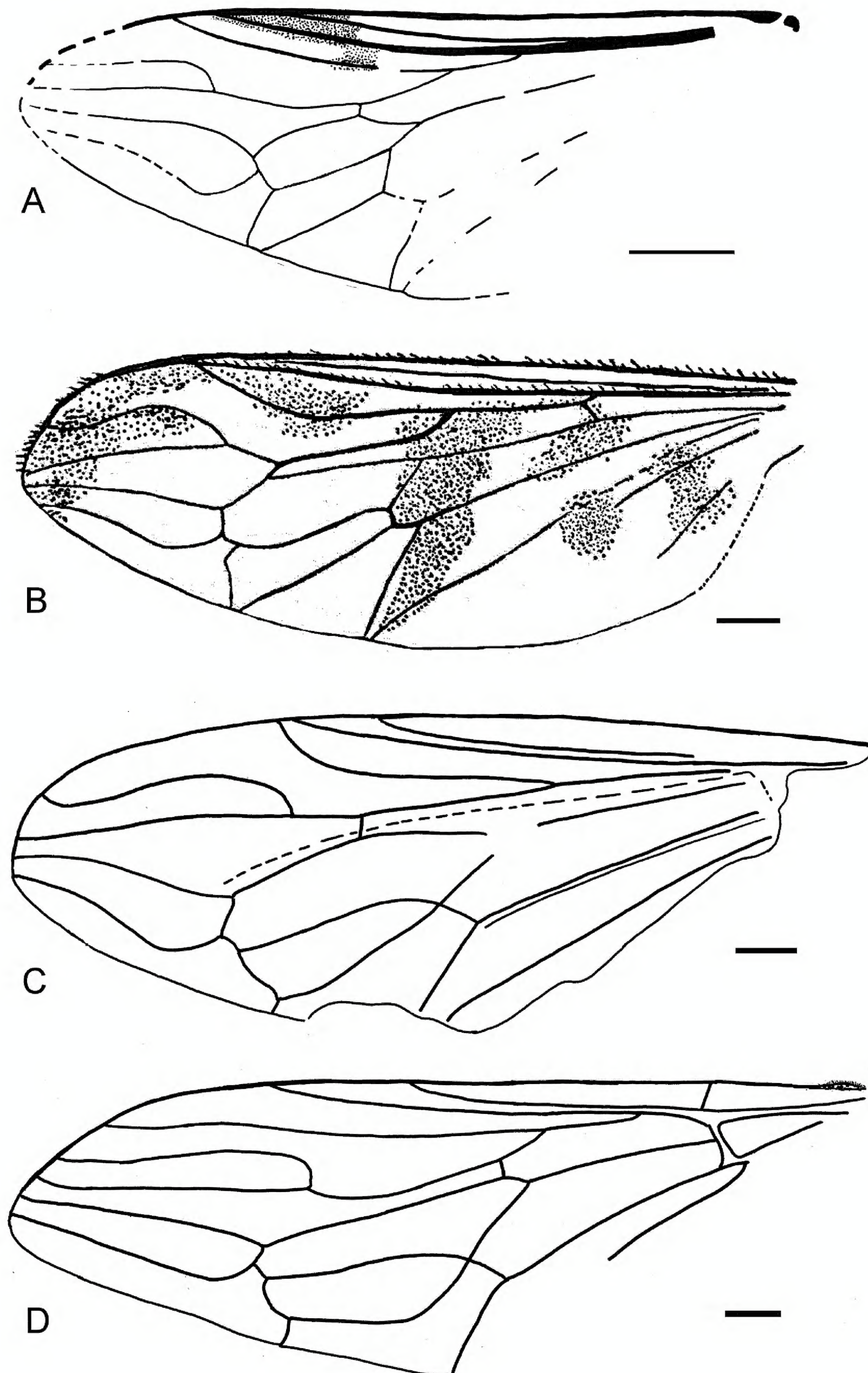


Figure 3. Difference and similarity between four sets of wings. Line drawings of holotypes. **A** *Sinonemestrius completus* sp. n., **B** *Sinonemestrius tuanwangensis* Hong & Wang, 1990 (after Hong and Wang 1990), **C** *Sinonemestrius akirai* Jarzembowski & Mostovski, 2000 (after Jarzembowski and Mostovski 2000), **D** *Ahirmoneura neimengguensis* K-y Zhang et al., 2008 (after K-y Zhang et al. 2008). Scale bars: 1 mm.

four times as long as wide; R4, R5, M1 and M2 slightly convergent, running towards wing tip (M1 ending just at wing tip); section of M3+4 slightly shorter than bM4; cell m3 nearly parallel quadrilateral but open apically; cell cu (traditionally anal cell) narrowly open. Legs with femora darkish brown, clavate, distinctly thicker than tibiae, tibiae and tarsi yellowish brown; femur of hindleg as long as, but twice as wide as, tibia, tibial spurs very short, distinctly less than tibial width, basitarsomere nearly as long as other tarsomeres combined, claw nearly as long as fifth tarsomere, empodium badly preserved, seemingly longer, but narrower, than pulvillus.

Abdomen ovate-oblong, with seven segments visible, clearly longer than head and thorax combined, with first segment longest, second segment widest, slightly wider than thorax; male genitalia longer than sixth segment with gonostylus (?) darkish brown, very narrow, strongly curved inwards.

Dimensions. Holotype: length of body 10.9 mm; head, 1.4 mm; thorax, 3.6 mm; abdomen 6.4 mm. Length of wing 7.4 mm, width of wing 2.9 mm.

Remarks. *Sinonemestrius completus* sp. n. differs from the type species *Sinonemestrius tuanwangensis* by the following features: R2+3 slightly curved, parallel to R1 and not meeting R1 end apically, fork of R4+5 distinctly distad to level of fork of M1+2, crossvein r-m meeting anterior margin of d cell basad to its midlength and wing membrane with a few markings (only limited to “Pt” and below it). On the other hand, this new species differs from *Sinonemestrius akirai* by Rs arising from R stem late (at about one-third of wing length vs near to wing base), the slightly curved R2+3 which runs parallel to R1 (vs R1 and R2+3 clearly convergent apically), fork of R4+5 distad (vs basad) to level of fork of M1+2 and cell m3 open (vs closed before hind margin of wing). Unfortunately, the body structures cannot be compared because the descriptions of the two known species are based on wing impressions.

Etymology. Latin, completus (complete), referring to the species erected based on a complete fly.

Holotype. No. NIGP L91803, a complete male fly, dorsoventral aspect, is held in the collection of NIGPAS.

Distribution. Type locality and horizon: Laiyang Formation, in the vicinity of Tuanwang, Laiyang, Shandong, China (Lower Cretaceous).

Repository. The Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Discussion

On the basis of a single wing of a fly from the Lower Cretaceous of the Laiyang Formation, Shandong, China, Hong and Wang (1990) erected the monotypic genus *Sinonemestrius*, which was originally placed in Nemestrinidae. Nagatomi and Yang (1998) erected a new monobasic family Sinonemestriidae for this genus. They considered it to be the sister group of Nemestrinidae. Judging from another find of a wing from the Lower Cretaceous of southern

England, Jarzembowski and Mostovski (2000) described a new species referring it to *Sinonemestrius* and retained Sinonemestriidae only as a tribe within Heterostominae, Xylophagidae; also, the diagnosis of *Sinonemestrius* was revised. Shortly after this study, Mostovski and Martínez-Delclòs (2000) transferred Heterostominae (including Sinonemestrine) into Rhagionemestriidae, another extinct family which is considered as a connecting link between Xylophagidae and Nemestrinidae. Nel (2010) agreed to the proposal (Mostovski and Martínez-Delclòs 2000) that *Sinonemestrius* belongs to Rhagionemestriidae. He moved the two modern genera (*i.e.* *Heterostomus* Bigot, 1857 and *Exeretoneura* Macquart, 1846) into Xylophagidae following Palmer and Yeates (2000) and Mostovski (2010 pers. comm.). Grimaldi (2016) also agreed with the placement proposed by Mostovski and Martínez-Delclòs (2000) that *Sinonemestrius* is a rhagionemestriid genus, but argued that Rhagionemestriidae is without question closely related to Acroceridae based on a distinct but very rare fly in late Cretaceous amber, while the modern genera *Heterostomus* and *Exeretoneura* appear to belong in the Tabanomorpha and Xylophagidae respectively, based on the studies of Coscarón et al. (2013) and Palmer and Yeates (2000).

The body structures and wing venation of *Sinonemestrius completus* sp. n. reveal that *Sinonemestrius* is very similar to the modern genus *Heterostomus*. This is based on the following synapomorphies: hemispherical head comprised mostly of the eyes; male holoptic; antennal flagellum with eight flagellomeres, stylus (or arista) absent; a pair of metatibial spurs present (although very small in *Sinonemestrius completus* sp. n.). In addition, there are close similarities in wing venation: wing membrane always with markings; C reaching wing tip, thinned behind wing tip; R2+3 ending close to R1 end; R4 sigmoidal; R5 aligned with stem of R4+5; R5 (or M1) ending at wing tip; crossvein r-m present; cell br very narrow, distinctly narrower than cell bm; discal cell usually narrow and long; cell m3 open (only closed in *Sinonemestrius akirai*); cell cu (traditionally anal cell) narrow and long (narrowly open in *Sinonemestrius*, closed in *Heterostomus*). For this reason, the proposal is supported here that *Sinonemestrius* could be related to heterostomid flies (Jarzembowski and Mostovski 2000, Mostovski and Martínez-Delclòs 2000). However, the placement of *Heterostomus* has been much debated. This genus includes only a single species, *Heterostomus curvipalpis* Bigot, 1857 from Chile. Lately, most works have classified it in Xylophagidae (Woodley 1989, Sinclair et al. 1994, Stuckenberg 2001, Kerr 2010); previously, it was included in various families within Tabanomorpha (Kröber 1930, Malloch 1932, Hennig 1972). Recently, the adult and pupa of *Heterostomus curvipalpis* were described and illustrated in detailed by Coscarón et al. (2013). They concluded that *Heterostomus curvipalpis* is related to Pelecorhynchidae within Tabanomorpha. Thus, it could be reasonable to retain Sinonemestriidae as a subfamily within Heterostomidae erected by Nagatomi (1977), and place these taxa in Tabanomorpha.

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